MORPHOMETRIC ANALYSES OF INTRODUCED AND ANCESTRAL POPULATIONS OF THE EURASIAN TREE SPARROW

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ABSTRACT.—Birds introduced into new environments by humans provide opportunity to assess microevolutionary change in morphology. The skeletal morphologies of introduced North American and ancestral German populations of the Eurasian Tree Sparrow (*Passer montanus*) were compared to assess: (1) the extent of morphometric differentiation between the introduced and ancestral populations, and (2) whether the introduced populations, which exhibited a decrease in genetic variability relative to the German population, display any such differences in morphometric variability. Sexual dimorphism in certain skeletal characters in *P. montanus* is interpreted to be a result of intraspecific interactions among males and adverse climatic conditions on both sexes. The smaller body size of North American *P. montanus* is thought to result either from interspecific interactions and/or flight habits different from their ancestral counterparts. Significant differences in bill morphology are found between German and North American *P. montanus*, which we believe reflect differences in diet. The North American population shows no significant decrease in intrinsic morphometric variation corresponding to the decrease in genetic variation demonstrated in comparison to German birds. *Received 13 Feb. 1990, accepted 13 April 1990.*

A few founding individuals may yield geographically isolated populations. Often little historical documentation of these founding events exists. As a result, details essential to studies of any morphometric and genetic differentiation between ancestral and introduced populations, e.g., time of separation (and hence time populations have had to diverge), may be lacking. Therefore, well-documented anthropogenic introductions of exotic species, e.g., the introduction of the Eurasian Tree Sparrow (*Passer montanus*) in North America, are important to the evaluation of microevolutionary processes. *P. montanus* was established in North America

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in 1870 when a bird dealer released 12 pairs of West German origin in Lafayette Park, St. Louis, Missouri (Lever 1987). After an early episode of population increase at St. Louis (Merrill 1876), the species began to spread slowly northward in neighboring Illinois. Numbers are now thought to exceed 150,000 in an area of ca 45,000 km^2 (St.Louis and Barlow 1987, 1988).

Comparisons of skin (Barlow 1973) and skeletal (Barlow 1980, Thompson 1983) characters between North American and German specimens showed that Illinois *P. montanus* were smaller than their European counterparts in certain skull and wing-pectoral girdle characters. Size differences between introduced and ancestral populations were attributed to ecological differences between the two areas (Barlow 1973, 1980). Recently we showed that North American *P. montanus* were less variable genetically than the ancestral German birds (St.Louis and Barlow 1988).

Genetic variation within introduced populations is often low following a founding event of a small number of individuals. As a result, introduced populations provide unique opportunities to test two predictions concerning the extent to which genetic variation governs variation in morphometric structure. Mayr (1954, 1963) predicted that low genetic variation should result in decreased morphometric variation. Contrary to Mayr, Lerner (1954) believed that heterozygosity leads to phenotypic stability (heterosis) and that populations with reduced genetic variation should show greater morphometric variation.

Morphometric variation in *P. montanus* was initially examined by Barlow (1980). He found that interpopulation variability (measured by coefficient of variation) was generally homogeneous across sexes and populations, with no evidence (except in wing length) of decreased variability in the North American population. Later, we found no statistically significant morphometric-genetic relationships among six populations of *P. montanus* when comparing: (1) morphometric 'size' with heterozygosity, and (2) estimated degrees of population differentiation using morphometric and genetic distance measures (St.Louis and Barlow 1987). At that time we did not, however, examine the intrinsic variation in morphometric characters of the North American and German birds needed to test the predictions of Mayr (1954, 1963) and Lerner (1954).

In the present study we replicate the earlier studies of Barlow (1980) and Thompson (1983), in an attempt to establish the extent of any further morphometric divergence between the introduced and ancestral populations of *P. montanus*. We also assess intrinsic morphometric variability, in terms of Mayr's or Lerner's predictions, in the North American birds already shown to have decreased genetic variability in comparison to German *P. montanus* (St.Louis and Barlow 1988).

TABLE 1

The Localities at Which *Passer montanus* were Obtained, Collection Dates, and Sample Sizes

Location	Latitude, longitude	Collection date (month/ year)	Sample sizes		
			Total	AM[a]	AF[b]
Karlshrule, West Germany	49.00N, 144.58E	11/84	30	8	10
Woodson, Illinois	39.40N, 90.35W	12/83	24	5	7
Naples, Illinois	39.45N, 90.35W	12/83	17	4	5
White Hall, Illinois	39.27N, 90.22W	01/85	52	24	15

[a] Adult males.
[b] Adult females.

METHODS

Specimen acquisition and preparation are detailed in St.Louis and Barlow (1987, 1988). North American populations were obtained between 1983 and 1985 from three sites in Illinois approximately 40–50 km apart (Woodson, Morgan County; Naples, Scott County; and White Hall, Greene County) (Table 1). Specimens representing the ancestral population were obtained in West Germany in 1985 from the region sampled by Barlow (1980) (Table 1). Acquisition of material was limited by permit restrictions.

Morphometric differentiation.—The 16 skeletal measurements previously used by Barlow (1980) and Thompson (1983) were taken only on the adult (skull completely ossified) *P. montanus* using dial calipers accurate to 0.05 mm (see St.Louis and Barlow 1987). Data from Illinois localities were pooled to minimize heterogeneity of variances resulting from the small sample sizes, and in turn tested for homogeneity of variances between the sexes and populations using the F_{max}-test (Sokal and Rohlf 1981) before using parametric statistical tests.

We tested for differences in skeletal features between the sexes in both the North American and German populations with one-way analyses of variance (ANOVA), performed using the SAS package of programs for personal computers (SAS Institute Inc. 1988). Differences between the German and North American populations for each sex were also assessed with ANOVA. However, the probability of incorrectly rejecting one or more true null hypotheses was high because of the large number of ANOVA tests done (16 skeletal characters for each hypothesis) (Rice 1989). Therefore, *P* values were adjusted to an overall $\alpha = 0.05$ level using the sequential Bonferroni method described by Rice (1989).

Morphometric and genetic variation.—Differences in 'intrinsic' or 'relative' variances for each mensural variable were compared for males and females between the German and North American populations in the manner of Lewontin (1966). Log_{10} transformed variables were used to give a measure of intrinsic variability, and in a multivariate extension of the Levene test (Van Valen 1978), following Fleischer et al. (1983) and Handford (1980), to test the hypothesis that the relative variances were equal between populations. Variables were log_{10} transformed to generate variances independent of their means (Sokal and Rohlf 1981). Differences in Levene values between the populations were examined by ANOVA.

Individual genotypes, obtained from 39 structural gene loci resolved by starch gel electrophoresis, were analyzed for allelic variation (St.Louis and Barlow 1988). There were no differences in allelic frequencies between age classes or the sexes for each locality; therefore, all specimens from a locality were pooled (St.Louis and Barlow 1988).

TABLE 2

MEAN (MM) AND STANDARD ERRORS OF SKELETAL MORPHOMETRIC CHARACTERS, AND
RESULTS FROM ANOVA BETWEEN THE SEXES IN GERMAN (A) AND NORTH AMERICAN (B)
POPULATIONS AND BETWEEN NORTH AMERICAN AND GERMAN FEMALE (C) AND MALE (D)
POPULATIONS OF *PASSER MONTANUS*

| | Germany | | | | North America | |
| | Females | | Males | | Females | |
Character	N	Mean ± SE	N	Mean ± SE	N	Mean ± SE
Premaxilla length	8	5.72 ± 0.09	10	5.81 ± 0.08	27	5.45 ± 0.05
Narial width	8	0.91 ± 0.02	10	0.92 ± 0.01	27	0.89 ± 0.01
Skull width	8	14.64 ± 0.12	10	14.86 ± 0.08	27	14.63 ± 0.06
Skull length	8	27.09 ± 0.19	10	27.32 ± 0.20	27	26.57 ± 0.11
Dentary length	8	5.13 ± 0.07	10	5.16 ± 0.06	27	4.84 ± 0.05
Mandible length	8	18.58 ± 0.18	10	18.59 ± 0.18	27	18.05 ± 0.07
Coracoid length	8	17.36 ± 0.15	10	17.92 ± 0.18	27	17.17 ± 0.09
Sternum length	8	20.58 ± 0.20	10	21.90 ± 0.22	27	20.76 ± 0.15
Keel length	8	19.26 ± 0.29	10	21.18 ± 0.31	27	19.27 ± 0.18
Sternum depth	8	9.93 ± 0.12	10	10.15 ± 0.11	27	9.41 ± 0.07
Humerus length	8	16.84 ± 0.19	10	17.37 ± 0.14	27	16.75 ± 0.09
Ulna length	7	18.47 ± 0.17	9	19.27 ± 0.15	27	18.17 ± 0.13
Femur length	8	16.56 ± 0.02	10	16.74 ± 0.11	27	16.68 ± 0.08
Femur width	8	1.19 ± 0.02	10	1.19 ± 0.01	27	1.16 ± 0.01
Tibiotarsus length	8	26.13 ± 0.28	10	26.49 ± 0.20	23	26.09 ± 0.15
Tarsometatarsus length	8	17.14 ± 0.15	10	17.50 ± 0.13	26	17.18 ± 0.13

* Significantly different when *P* values were adjusted to an overall $\alpha = 0.05$ level using the sequential Bonferroni method (Rice 1989).

Wilcoxon's paired signed rank test (Sokal and Rohlf 1981) was employed to measure differences in genetic variation between the German and North American populations. Heterozygosity (direct count) and number of alleles per locus served as measures of genetic variation. Heterozygosity for each locus and number of alleles for each locus were paired for the above testing.

RESULTS

Morphometric differentiation. —Results of the F_{max}-tests showed no significant heterogeneity of variances between the sexes for any skeletal variable in the German or North American populations at the $P \leq 0.05$ level. In male and female samples, only femur width showed a significant heterogeneity of variances between populations for the skeletal variables ($F = 3.17$, df = 7, 26, $P = 0.03$). The significant heterogeneity of variances seen here for only femur width could be attributed to a Type I error (rejection of true null hypothesis). We therefore proceeded with parametric statistical analyses.

ANOVA showed several skeletal measurements in the German and

TABLE 2
CONTINUED

North America Males		A		B		C		D	
N	Mean ± SE	F	P > F	F	P > F	F	P > F	F	P > F
33	5.57 ± 0.04	0.59	0.453	3.21	0.079	6.13	0.019	8.88	0.005
33	0.87 ± 0.01	0.10	0.761	3.30	0.074	0.44	0.514	6.29	0.016
33	14.69 ± 0.05	2.47	0.136	0.58	0.449	0.00	0.962	2.96	0.093
33	26.73 ± 0.07	0.71	0.412	1.54	0.220	5.19	0.029	12.11	0.001*
32	4.98 ± 0.05	0.09	0.762	3.79	0.056	10.22	0.003*	3.43	0.072
32	18.16 ± 0.07	0.00	0.967	1.03	0.314	10.88	0.002*	6.97	0.012
33	17.52 ± 0.08	5.46	0.033	8.40	0.005	1.18	0.285	5.10	0.029
33	21.14 ± 0.12	18.27	0.001*	3.86	0.054	0.38	0.543	9.43	0.004*
33	19.92 ± 0.14	19.83	0.000*	8.19	0.006	0.00	0.982	16.49	0.000*
33	9.73 ± 0.05	1.84	0.194	14.60	0.000*	12.65	0.001*	15.35	0.000*
33	17.00 ± 0.08	5.69	0.030	4.51	0.038	0.21	0.648	5.30	0.027
33	18.56 ± 0.10	12.22	0.004*	6.24	0.015	1.33	0.257	12.01	0.001*
33	16.71 ± 0.07	0.88	0.361	0.13	0.721	0.46	0.504	0.05	0.823
33	1.16 ± 0.01	0.02	0.888	0.14	0.711	3.40	0.074	4.11	0.049
32	26.02 ± 0.14	1.18	0.294	0.31	0.578	0.02	0.890	1.10	0.300
33	17.27 ± 0.11	3.33	0.087	0.32	0.572	0.03	0.855	1.18	0.285

North American populations to be significantly larger in males than in females when P values were adjusted using the sequential Bonferroni method (Table 2). Two body core (sternum and keel length) and one wing (ulna length) characters were significantly different between the sexes in German birds. Sternal depth only, however, was significantly different between the sexes in North American birds. As a consequence, the sexes were treated separately in all remaining analyses.

Three and five of the 16 characters in females and males, respectively, were significantly smaller in the North American population when P values were again adjusted using the sequential Bonferroni method (Table 2). Two skull (dentary and mandible length) and one body core (sternum depth) characters were smaller in North American females, whereas one skull (skull length), three body core (sternum and keel length, and sternum depth), and one wing (ulna length) characters were smaller in North American males.

Morphometric and genetic variation. — Using the method of Lewontin (1966), only skull length in males and femur width in females showed a

TABLE 3

VARIANCE OF LOG-TRANSFORMED SKELETAL CHARACTERS AND RESULTS OF SIGNIFICANCE
TESTS OF LEWONTIN (1966) USED TO DETERMINE DIFFERENCES IN INTRINSIC VARIATION
BETWEEN NORTH AMERICAN AND GERMAN FEMALE SKELETAL CHARACTERS IN
PASSER MONTANUS

Character	Germany		North America		s^2 (larger) / s^2 (smaller)	df	$F_{0.05}$
	N	$s^2 \log_{10} x$ $(\times 10^{-4})$	N	$s^2 \log_{10} x$ $(\times 10^{-4})$			
Premaxilla length	8	3.26	27	5.19	1.59	26, 7	3.40
Narial width	8	9.31	27	9.03	1.03	7, 26	2.39
Skull width	8	1.02	27	0.79	1.29	7, 26	2.39
Skull length	8	0.71	27	0.86	1.21	26, 7	3.40
Dentary length	8	3.12	27	4.41	1.41	26, 7	3.40
Mandible length	8	1.46	27	0.74	1.97	7, 26	2.39
Coracoid length	8	1.10	27	1.24	1.13	26, 7	3.40
Sternum length	8	1.40	27	2.72	1.94	26, 7	3.40
Keel length	8	3.26	27	4.41	1.35	26, 7	3.40
Sternum depth	8	2.36	27	2.80	1.19	26, 7	3.40
Humerus length	8	1.93	27	1.43	1.35	7, 26	2.39
Ulna length	7	1.09	27	2.49	2.28	26, 6	2.83
Femur length	8	1.51	27	1.10	1.37	7, 26	2.39
Femur width	8	5.99	27	1.86	3.22*	7, 26	2.39
Tibiotarsus length	8	1.69	23	1.36	1.25	7, 22	2.46
Tarsometatarsus length	8	1.22	26	2.58	2.11	25, 7	3.41

* $P \leq 0.05$.

significant decrease ($P \leq 0.05$) in intrinsic variation in the North American
P. montanus in comparison with German birds. Variation in all other
characters in both populations was highly similar (Tables 3 and 4). An
ANOVA on Levene variables demonstrated equal variation between the
populations for both male ($F = 1.46$, df = 1, 41, $P = 0.23$) and female
($F = 0.32$, df = 1, 33, $P = 0.57$) specimens.

Mean heterozygosity was 0.079 (SE = 0.025, N = 93) in North American
specimens and 0.093 (SE = 0.026, N = 30) in German specimens. Mean
number of alleles per locus was 1.4 (SE = 0.1) in the North American
specimens and 1.5 (SE = 0.1) in the German specimens. For these two
measures of genetic variation, Wilcoxon's paired signed rank test indi-
cated a significant difference between the German and North American
populations only for mean number of alleles per locus ($T_s = 4$, $P = 0.05$).

DISCUSSION

Morphometric differentiation. —When assessing morphology of a spe-
cies which exhibits sexual dimorphism, each sex must be analyzed sep-

TABLE 4

VARIANCE OF LOG-TRANSFORMED SKELETAL CHARACTERS AND RESULTS OF SIGNIFICANCE TESTS OF LEWONTIN (1966) USED TO DETERMINE DIFFERENCES IN INTRINSIC VARIATION BETWEEN NORTH AMERICAN AND GERMAN MALE SKELETAL CHARACTERS IN *PASSER MONTANUS*

Character	Germany		North America		$\dfrac{s^2 \text{ (larger)}}{s^2 \text{ (smaller)}}$	df	$F_{0.05}$
	N	$s^2\log_{10}x$ $(\times 10^{-4})$	N	$s^2\log_{10}x$ $(\times 10^{-4})$			
Premaxilla length	10	3.71	33	3.11	1.92	9, 32	2.19
Narial width	10	4.52	33	9.92	2.19	32, 9	2.85
Skull width	10	0.52	33	0.67	1.28	32, 9	2.85
Skull length	10	1.03	33	0.45	2.29*	9, 32	2.19
Dentary length	10	2.82	32	6.76	2.39	31, 9	2.86
Mandible length	10	1.73	32	1.00	1.73	9, 32	2.20
Coracoid length	10	1.81	33	1.44	1.26	9, 32	2.19
Sternum length	10	1.97	33	1.92	1.03	9, 32	2.19
Keel length	10	3.99	33	3.19	1.25	9, 32	2.19
Sternum depth	10	2.06	33	1.60	1.29	9, 32	2.19
Humerus length	10	1.11	33	1.41	1.27	32, 9	2.85
Ulna length	9	1.07	33	1.80	1.68	32, 8	3.07
Femur length	10	7.90	33	1.00	1.27	32, 9	2.85
Femur width	10	1.86	33	3.34	1.80	32, 9	2.85
Tibiotarsus length	10	1.03	32	1.72	1.67	31, 9	2.86
Tarsometatarsus length	10	1.09	33	2.54	2.33	32, 9	2.85

* $P \leq 0.05$.

arately when: (1) differences in morphology at the interpopulation level are examined, and (2) forces which may have led to the differentiation between the populations are investigated (Price 1984). Determining how the two sexes in any population respond to environmental parameters in effect assesses the cause and perpetuation of dimorphism of secondary characteristics (Price 1984).

Three sternal and wing characters were significantly smaller in females than in males in the German population, whereas only sternum depth was significantly different between the sexes in the North American population. Differences in size between the sexes in the closely related House Sparrow (*Passer domesticus*) are thought to reflect selection favouring large males in male to male interactions (sexual selection) (e.g., Johnston and Selander 1971, Johnston 1973, Johnston and Fleischer 1981) but may be modified by differential selection of body size classes of males and females during adverse climatic conditions (e.g., Johnston 1969, Johnston et al. 1972, Fleischer and Johnston 1982; also see McGillivray and John-

ston 1987). For example, the larger dominant males within a population are also at a selective advantage with respect to thermoregulation (small surface area to volume ratio) during severe winter storms (Johnston and Selander 1973), whereas large subadult females are probably selected against (McGillivray and Johnston 1987).

Bill size is believed to be correlated with food size and other aspects of foraging (e.g., Hespenheide 1973; Abbott et al. 1975, 1977; Schluter and Grant 1984). We detected, however, no sexual size dimorphism in bill characters in North American *P. montanus contra* Thompson (1983), or in the German birds. Thompson (1983) thought that bill dimorphism was related to the influence of environmental parameters affecting females only (mean July temperature [e.g., Johnston 1969]) and possibly because of a broader spectrum of food resources in North America relative to Germany. Because bill size of males and females is similar in both the North American and German populations of *P. montanus,* we assume that the sexes have not diverged in resource use (i.e., exploitation of different niches).

Head- and bill-related characters, however, differed significantly for both males and females between North American and German birds. The differences found here between certain North American and German head- and bill-related characters in males were not found by Barlow (1980) or Thompson (1983), suggesting that the foraging-related differences noted herein were not previously recognized. In winter in North America, *P. montanus* was seen feeding virtually 100% of the time on cereal grains (corn, wheat, soybeans, and livestock feed) (pers. obs.). This diet differs from that of *P. montanus* in Germany where winter food consisted of 79% seeds of weeds, 9.6% cereal (oats, barley, wheat), 8.4% vegetal parts, and 3% glumes and plant fibers (Keil 1973). In summer, North American *P. montanus* fed on different arthropod prey than did European *P. montanus* (Anderson 1973, 1984).

Foraging-related differences between North American and German *P. montanus* may be attributed further to interactions between *P. montanus* and *P. domesticus.* The population size increase and aggressiveness of North American *P. domesticus* may have contributed to the slow rate of population growth of *P. montanus* (Summers-Smith 1988). Anderson (1973) demonstrated a syntopic relationship between *P. montanus* and *P. domesticus* in North America which differs from the interactions of the two species in most of Eurasia (Summers-Smith 1988, Lack 1971, Dyer et al. 1977, Anderson 1984). Winter diet and foraging sites for both *Passer* species resembled each other closely in North America, where both species often feed together in large mixed flocks (Anderson 1973, pers. obs.). In West Germany, however, winter foraging sites differed between

P. montanus and *P. domesticus* (Keil 1973). The relative size of winter food items of the two species is unknown. *Passer montanus* summer diet overlapped with that of *P. domesticus* to a greater extent in North America than in Europe (Anderson 1984). Anderson (1980), however, documented a similarity in summer food size in North America between *P. domesticus* and *P. montanus,* suggesting that these two species do not separate resources by size. We assume, therefore, that change in bill morphology in *P. montanus* is not related to interspecific interactions with *P. domesticus* on summer diet.

A significant decrease in sternal depth contributed to the degree of size reduction in both male and female North American specimens when compared with German adults. North American males, however, have shown a significant decrease in other sternal- and wing-related characters in comparison with German specimens not seen in females. These differences, previously explained in terms of flight constraints (i.e., migration; Barlow 1980), might also be attributable to interspecific interactions between *P. montanus* and *P. domesticus*. In North America, *P. domesticus* is known to displace *P. montanus* from nest sites (Widmann 1889, pers. obs.). Anderson (1973) demonstrated experimentally in Missouri that the larger *P. domesticus* excluded the smaller *P. montanus* from nest boxes with hole dimensions large enough for both species to enter. Perhaps then some modicum of selection for smaller body size (sternal and wing characters) might be attributable to size of opening of nest cavities, especially in males, because males both choose and initially defend the nest site (Anderson 1973). The decrease in sternal depth of North American females suggests that they have responded in a similar manner in favoring nest cavities with a small entrance.

In the present study, we found no significant differences between North American and German birds for any leg-related characters, *contra* Barlow (1980). Barlow (1980) attributed significantly smaller leg characters in North American *P. montanus* to possible perching-related differences between North American and German birds or character covariation in the inherently smaller North American specimens.

Morphometric and genetic variation.—Although we found only a trend toward decreasing heterozygosity in North American compared with German populations, there was a significant pairwise decrease in mean number of alleles per locus in the North American population. Such a pattern of genetic variation may result from the effects of a bottleneck in population size on the mean number of alleles per locus and heterozygosity in a population (Nei et al. 1975). In general, mean heterozygosity is expected to increase faster in a population than mean number of alleles, the former resulting from effective population size and rate of increase following the

founding event and the latter being a function of the mutational rate (Nei et al. 1975; also see St. Louis and Barlow 1988).

Mayr (1954, 1963) predicted that following a founding event or genetic bottleneck, a reduction in genetic variation would produce a decrease in morphometric variation apparent in the founder population. Lerner (1954), on the other hand, proposed that highly heterozygous individuals have enhanced developmental homeostasis, resulting in a reduction of morphometric variation. We detected no evidence in support of Mayr's (1954, 1963) or Lerner's (1954) predicted relationships. Only skull length in males and femur width in females showed a significant decrease in intrinsic variation in the North American population which might correspond to the observed reduction in allozyme variation. Because these significant differences appear to be isolated cases, it is presumed they are of little genetic significance. These results correspond to those already discussed, in which selection, both natural and sexual, acts on the morphometric characters to produce a mean optimal phenotype. This optimal phenotype most likely has a corresponding standard amount of intrinsic variation about its mean. This standard amount of variation has also been noted for example in introduced North and South American populations of *P. domesticus* as compared with ancestral European populations (Johnston and Klitz 1977), in the Fox Sparrow (*Passerella iliaca*) (Zink et al. 1985), and in the Rufous-collared Sparrow (*Zonotrichia capensis*) (Handford 1980).

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JOINT MEETING OF THE COOPER ORNITHOLOGICAL SOCIETIES

Three special events are tentatively scheduled for the joint meeting of the Cooper and Wilson Ornithological Societies 15–19 May 1991, at Norman Oklahoma: (1) a symposium on the Interface of Science and Conservation in Latin American Ornithology, (2) a symposium on the effects of Forest Fragmentation on Birds, and (3) a workshop on Endangered Passerines.